Temporal changes in benthic ostracode assemblages in the Northern Bering and Chukchi Seas from 1976 to 2010

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ABSTRACT

We analyzed living ostracode assemblages from the northern Bering Sea, collected between 1976 and 2010, and from the Chukchi Sea, collected in 2009 and 2010, to examine how climatic and oceanographic changes are affecting modern ostracode species distributions. Totals of 21 and 28 ostracode species were identified, respectively, from Bering and Chukchi Sea surface sediment samples. The Bering Sea assemblage is largely transitional in species composition between those inhabiting western Arctic continental shelves and the subarctic Gulf of Alaska. Temporal changes in the Bering Sea assemblage provide evidence that decadal temperature changes have affected species composition. For example, the proportion of *Normanicythere leioderma*, a predominantly Arctic species, decreased from 70% of the total assemblage population in 1999 to 15% by 2006. This decrease coincided with a shift in the Arctic Oscillation toward a positive mode and warmer Bering sea-surface temperatures (SST) beginning in the early 2000s. In contrast, the more temperate species, *Pectocythere janae* (also known as *Kotoracythere arctoborealis*) made up less than 4% of the Bering assemblage prior to 2000 but increased in abundance to as much as 30% as Bering Sea temperatures rose from 2001 to 2006. This pattern has reversed since 2006 when cooler temperatures led to a decline in *P. janae* and return in the prominence of *N. leioderma*. Our results support the idea that recent ocean temperature changes and a reduced sea-ice season in the Bering–Chukchi Sea region are changing species composition in benthic ecosystems.

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1. Introduction

As surface temperatures rise in the Arctic Ocean and sub-polar seas, satellite observations document a corresponding reduction in the extent, thickness, and duration of seasonal sea-ice cover (Stroeve et al., 2008) and a potential increase in primary production as a result of greater light penetration into sea ice-free waters (Pabi et al., 2008). In recent years, Arctic multi-year ice has declined by almost 50% in extent, and fall freeze-up occurs later in the year (Serreze et al., 2007; Stroeve et al., 2008). Model results indicate these trends will continue, and that the Arctic Ocean might become predominantly ice-free in summer in a few decades (Wang and Overland, 2009). Sea-ice retreat has been particularly dramatic in the Arctic Ocean just north of the Bering Strait; sea-ice retreats in 2007 and 2009 lengthened the

open-water season by about four weeks compared with a decade ago (Grebmeier et al., 2010).

While these patterns of sea-ice decline are well documented, much less is known about the responses of biological communities to ice cover changes. According to Yasuhara et al. (2012a) sea-ice cover is an important factor controlling benthic faunal distributions and species diversity. Here we present new data on benthic ostracode distributions from the Chukchi Sea continental shelf, the Chirikov Basin of the northern Bering Sea, and the area south of St. Lawrence Island (Fig. 1). Ostracodes have environmentally sensitive distributions, and water temperature is one of the most influential factors controlling reproduction, survival, geographic distribution and diversity (Hutchins, 1947; Smith and Horne, 2002; Yasuhara et al., 2009). Ostracodes are meiobenthic, bivalved Crustacea, and have several distinct advantages for retrospective ecosystem studies. Their calcium carbonate shells are preserved in marine sediments enabling species identification from shell morphology, even after their soft parts decompose. Unlike macrofaunal species, which cannot be analyzed quantitatively in sediment cores because of their size and scarcity, adult ostracodes range in size from 0.5 mm to 2 mm and can be quantified in small samples available from individual grab and/or

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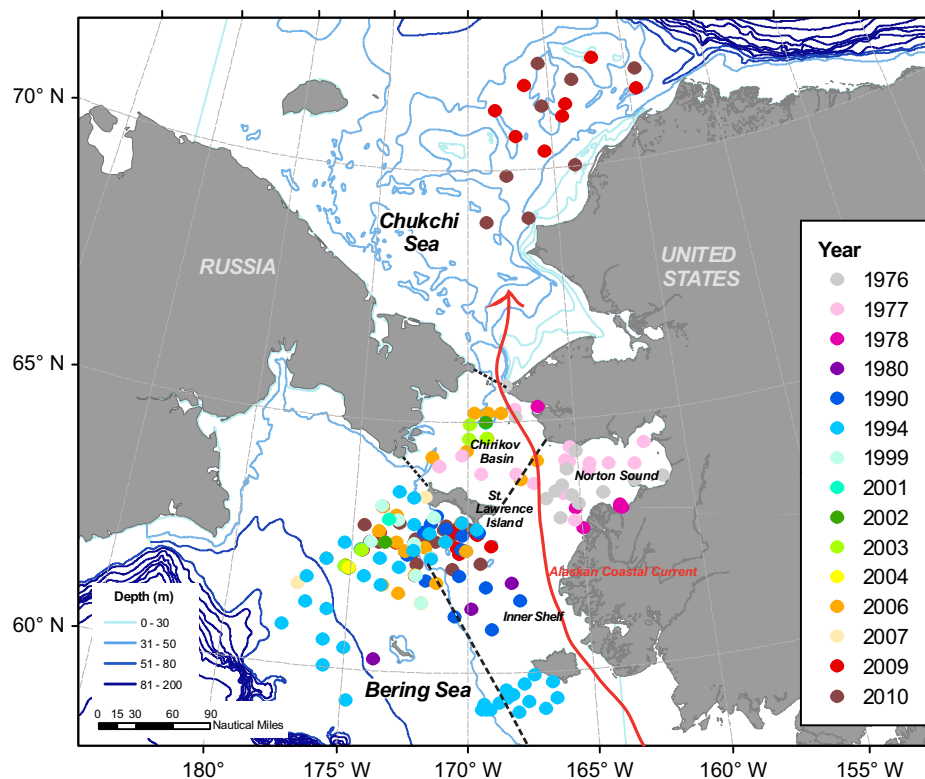jgrebmei@umces.edu (J.M. Grebmeier).

Fig. 1. Bathymetry of the Bering and Chukchi seas and locations of 225 Bering Sea and 18 Chukchi Sea surface sediments analyzed in this study, color-coded by year of collection.

core samples. Moreover, marine ostracode species have bio-geographical and ecological limits controlled by temperature, salinity, or nutrient/food availability (Cronin et al., 2010a; Stepanova et al., 2007; Yasuhara et al., 2012a). Consequently, these crustaceans are used extensively in paleoecology and paleoclimatology to document climatically driven changes in ocean temperature, circulation, salinity, and ocean productivity (e.g.; Cronin et al., 1994, 1996, 2005, 2010b; Didié and Bauch, 2000; Yasuhara et al., 2012a, 2012b). In this study, we sought to determine whether recent changes in temperature and ice cover in the Bering Sea have affected species distributions. To the best of our knowledge, this is the first published report on modern ostracode fauna from the northern Bering shelf. Adjacent areas where ostracode data are available include the Arctic Ocean (Cronin et al., 2010b) including the Chukchi/Beaufort Seas to the north of Bering Strait (Joy and Clark, 1977) and the Gulf of Alaska to the south of the Bering Sea (Brouwers, 1990; 1993; 1994).

1.1. Environmental setting

The Bering and Chukchi Seas are among the world's most productive ecosystems supporting high, seasonal primary productivity that exceeds $1 \, gC \, m^{-2} \, d^{-1}$ during the spring bloom (Brown et al., 2011; Springer et al., 1996) as well as diverse invertebrate, fish, seabird, and marine mammal populations (National Research Council, 1996). About 50% of the Bering Sea is a wide continental shelf to the north and east, which is less than 200 m in depth (Brown et al., 2011). This shelf extends through the Bering Strait into the Chukchi continental shelf in the western Arctic Ocean.

The Bering Sea is located in a transition region between a generally cold, dry Arctic air mass to the north and moist, relatively warm air to the south (Mantua and Hare, 2002). Hunt and Stabeno

(2002) concluded that the southeastern Bering Sea climate is jointly influenced by both the Pacific Decadal Oscillation (PDO) and the Arctic Oscillation (AO). The PDO is a multi-decadal pattern of Pacific climate variability involving air–ocean interactions that create current and sea surface temperature changes in the North Pacific (Mantua and Hare, 2002). In contrast, the northern Bering Sea, which we define as the shelf north of St. Matthew Island (approximately 61–65°N), and the Chukchi Sea are more directly influenced by the AO (Grebmeier et al., 2006a, 2006b). The state of the AO is determined by the atmospheric pressure gradient in the high Arctic, and it alternates between negative (high pressure over the North Pole) and positive (low pressure) modes. This coupled air–sea interaction is closely linked to the strength and position of the Beaufort Gyre in the Arctic Ocean. From 1989 to 2006, the AO was predominantly in a positive mode, causing lower Arctic air pressure and higher sea surface temperatures in the Arctic Ocean (Overland et al., 2008). NOAA's Climate Prediction Center (http://www.cpc.ncep.noaa.gov/) indicates that the AO has been in a negative mode for the period 2009–2010 but has exhibited an overall positive trend since 1989.

These air–sea interactions, and also anthropogenic factors, have contributed to interannual and decadal changes in temperature and sea ice in the North American Arctic over the last several decades (Overland et al., 2008; Serreze et al., 2007). These changes have happened in the context of general circulation in the Bering and Chukchi Seas, which is influenced by three north-ward flowing water masses arrayed east to west: less saline and nutrient-poor Alaska coastal water (Fig. 1); a mixed, more saline Bering Shelf water mass to the west; and a seasonally cold and even more saline Anadyr water mass further to the west (Stabeno et al., 2007; Belkin et al., 2009). As these water masses extend into the Chukchi Sea, the differences between the mixed shelf water and Anadyr water become less distinct; and there are also

differences in temperature, nutrients and salinity depending upon the season when N. Bering Sea water passes through Bering Strait (Cooper et al., 2013).

One example of recent change is the duration of the open water season. The Chirikov Basin, located to the north of St. Lawrence Island and extending to Bering Strait, has had an open-water season increase of 25 days during the past 25 years (Fig. 2). (The Chirikov Basin is bounded by St. Lawrence Island to the south, the Chukotka peninsula to the west, the Seward peninsula to the east, and Bering Strait to the north.) This has changed not only the timing of when primary productivity peaks but may also increase production due to a longer, sustained bloom (Arrigo et al., 2008; Brown et al., 2011; Brown and Arrigo, 2012). In the Bering and Chukchi Sea region, ecosystem reorganization (also called a regime shift, Bluhm and Gradinger, 2008; Hare and Mantua, 2000) may be related to changing seasonal sea-ice conditions, which can alter benthic-pelagic ecosystem processes and cause a cascade of consequences through the food web (Grebmeier et al., 2006a). Biological observations in these areas have documented changes in species composition and northward range extensions for zooplankton, bottom-dwelling organisms and fish that may collectively signify a large, climate-driven ecosystem reorganization (Grebmeier, 2012; Mueter and Litzow, 2008).

Despite these changes in the northern Bering Sea and Chukchi Sea, it is important to note that similar sea-ice changes are not being consistently observed further to the south in the Bering Sea (Stabeno et al., 2012). In winter, the southern margin of sea-ice coverage in the Bering Sea reaches an annual maximum by March, but sea ice is in part uncoupled from sea-ice retreat to the north because of the semi-enclosed nature of the marginal sea. Ice duration in the southern Bering Sea and along the continental margin, although varying from year to year, has not consistently changed over the time period we consider here (Fig. 2; Brown et al., 2011).

2. Materials and methods

2.1. Ostracode sampling

A total of 225 northern Bering Sea surface sediment samples containing 5972 ostracode valves and carapaces were collected during a number of cruises from 1976 to 2010 (Table 1). Most samples came from the central and northern Bering Sea continental shelf, with additional samples from Norton Sound collected in 1976–1978 (Fig. 1). The 1977 cruise also included sampling locations in the Chirikov Basin, immediately north of St. Lawrence Island. Sixteen surface sediment samples from the Chukchi shelf contained 1198 specimens. Samples were collected from water depths ranging from 10 to 110 m and were taken from
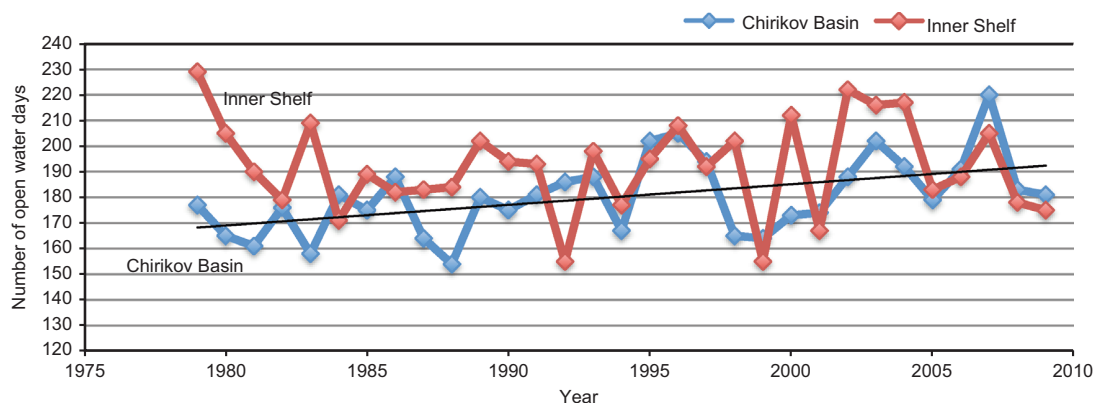

Fig. 2. Number of open water days (reflecting length of ice-free period) in the Chirikov Basin (blue line) and along the Inner shelf (red line), 1979–2009. The trend line shows open water duration in the Chirikov Basin (north of St. Lawrence Island) has increased over these three decades, accounting for an ice loss of $\sim 77 \pm 37$ km^2 of ice per year, with ice exiting by mid-June (Brown et al., 2011). "Open water" is defined as a satellite-derived sea-ice concentration below 10%. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)

Table 1
Listing of research cruises by year, month, ship, and region, from which samples for this study were collected.

Year	Month	Ship	Region
2010	March	USCGC Polar Sea	South of St. Lawrence Island
2009	March	USCGC Healy	South of St. Lawrence Island
2007	May–June	USCGC Healy	Chirikov and South of St. Lawrence Island
2006	May–June	USCGC Healy	Chirikov and South of St. Lawrence Island
2004	July	CCGS Sir Wilfrid Laurier	Chirikov and South of St. Lawrence Island
2003	July	CCGS Sir Wilfrid Laurier	Chirikov and South of St. Lawrence Island
2002	July	CCGS Sir Wilfrid Laurier	Chirikov and South of St. Lawrence Island
2001	July	CCGS Sir Wilfrid Laurier	Chirikov and South of St. Lawrence Island
1999	April	USCGC Polar Sea	South of St. Lawrence Island
1994	May–June	RV Alpha Helix	South of St. Lawrence Island
1990	June	RV Alpha Helix	South of St. Lawrence Island
1980	August	Samuel Phillips Lee	South of St. Lawrence Island
1978	August–September	Sea Sounder	Norton Sound, Bering
1978	July	Karluk	Norton Sound, Bering
1977	July–August	Sea Sounder	Chirikov and Norton Sound
1976	March	Sea Sounder	Chirikov and Norton Sound
2009	July–August	RV Alpha Helix	Chukchi
2010	July–August	RV Moana Wave	Chukchi

the top of Van Veen grabs before the grab was opened, or from the top of HAPS (a frame-supported bottom corer) and box corers.

Sediments ranged from silty clay to sand. Ostracodes were generally more abundant in silty clay sediments than in coarser sandy sediments, which likely results from slower deposition in more hydrodynamically active areas.

We assume that ostracode assemblages preserved in continental shelf surface sediments in this region are organisms that were living at or shortly before the time of collection. This assumption is supported by [7]Be data in sediment cores that were collected from the Canadian Coast Guard Service vessel Sir Wilfrid Laurier in July 1998 at six stations in the Chukchi Sea north of Bering Strait that have been incorporated into a Distributed Biological Observatory for the Pacific Arctic region (Grebmeier et al., 2010). These data indicate that this atmospherically derived radionuclide ([7]Be, half-life 53d) is present in the surface 0–1 cm sediments and was not detected at all at depths of 4 cm or greater (L.W. Cooper, unpublished data).

With a few exceptions, the ostracode data we report here involved spring and summer cruise collections. Sometimes the shells of molts or dead specimens from prior years are also recovered. In the case of Bering Sea ostracodes, most assemblages included adult specimens and juvenile molts, and 60% of the specimens were articulated carapaces, or carapaces with chitinous appendages. A few samples contained Rose bengal-stained specimens. Rose bengal stains cytoplasm, so this method can help distinguish specimens that were alive at the time of collection. A few reworked specimens from prior years, identified by broken or abraded specimens, are expected in a continental shelf setting. Thus, we consider the faunal data presented here to be largely representative of the live species assemblages present at the time that the ostracode samples were collected. We expect that these species assemblage data will be useful for detecting decadal and, in some cases, large interannual changes in the ecosystem.

2.2. Sample processing

Ostracodes were separated from 20 to 100 g sediment aliquots by washing the samples with tap water through a 63-µm sieve. Samples were then dried in a convection oven at 50 °C for 12–24 h. The > 63-µm size fraction includes adults and most juvenile molts of all species. Ostracodes were picked from the > 125 µm sediment size fractions with a fine, damp brush under a light microscope and placed on slides. The > 125 µm fraction is conventionally used because ostracode carapaces are usually larger than this, with the exception of some early instars. Species were identified primarily following the taxonomy and scanning electron microscope (SEM) imagery provided in Stepanova et al. (2007) and Brouwers (1990, 1993, 1994). Identification is based primarily on physical features such as carapace morphology (shape and size), pore size, and pore distribution, hinge characteristics, and shell ornamentation.

Species abundances (relative frequencies), which we define as the percentage of each species of the total ostracode assemblage, were calculated for each sample. Abundances were computed by dividing the number of individual species found in each sample by the total number of specimens found in that sample and then multiplying the result by 100 to convert to percent. Density was calculated by dividing the total number of ostracode specimens found in each sample by the dry sediment weight (grams) of that sample.

2.3. Sources of temperature and sea-ice data

Mean summer Sea Surface Temperature (SST) data (1982–2009) for the Chirikov Basin and Inner Shelf regions are based on the Reynolds Optimum Interpolation SST (OISST) Version 2 product derived from the Advanced Very High Resolution Radiometer (AVHRR) at 0.25° resolution available from NOAA (Brown et al., 2011). We used the geographic boundaries for the Chirikov Basin and Inner Shelf regions defined in Brown et al., 2011, Fig. 1. For these two regions, depth averages between 0 and 50 m. "Summer" is defined as July, August and September. Annual mean Bering Sea summer bottom water temperatures (BWT) and May SST (Fig. 5A) were obtained from the Bering Climate and Ecosystem data archive (http://www.beringclimate.noaa.gov/data/). BWT data were collected from bottom trawl surveys across the eastern Bering Sea shelf from early June to early August, during the years 1982–2007. The spatial coverage spans approximately latitudes 54.5–62°N and longitudes 179–158°W, with stations gridded at roughly 20 nautical miles distance (248–317 stations/yr).

The May SST data from the southeastern Bering Sea (defined as 54.3–60.0°N, 161.2–172.5°W) is probably the best long-term regional water temperature data set. These data were summarized in the NCEP/NCAR Reanalysis project (Kalnay et al., 1996). Index values of the data are defined as deviations from the mean value (2.48 °C) for the 1961–2000 period normalized by the standard deviation (0.73 °C). We recognize that the northern and southern Bering Sea regions have different temperature histories, with more seasonality in the north due to greater surface warming from the influence of Alaska Coastal water (Fig. 1). Because the central-northern Bering Sea is shallow (< 50 m) and well mixed, SST and BWT patterns generally show broad decadal patterns but do not provide year- and site-specific temperature data for our study region or precise temperature ranges that ostracode species require. Nonetheless, the southeastern Bering record is the best available annual spring–summer record covering the study period and appears to represent regional temperature patterns for the last few decades.

2.4. Statistical analyses

All statistical tests were performed with PAST (PAleontological Statistics; Hammer et al., 2001). PAST is a comprehensive statistics package that runs a range of standard numerical analysis and operations used in quantitative paleontology and many sub-fields of earth science. Several multivariate techniques (cluster, detrended correspondence and canonical correspondence analyses) were used to provide a consistent way to search for distributional patterns.

3. Results

3.1. Bering Sea assemblage composition

A total of 21 species (Fig. 3) were identified in the Bering Sea representing a mixture of Arctic and subarctic species. The dominant taxa were Normanicythere leioderma, Sarsicytheridea bradii, Semicytherura complanata, and Pectocythere janae. While varying in relative abundance from year-to-year, these four species cumulatively make up 72% of all specimens identified. During the 34-year time span of this study, average ostracode density was 3.18 specimens per gram of dry sediment. The number of individuals fluctuated widely from sample to sample, from a few specimens to several hundred.

3.2. Cluster analysis

We used PAST to perform an R-mode cluster analysis with a Euclidean similarity measure to sort species with similar patterns of abundance into separate groups (Fig. 3). Using all samples (n = 225), a dendrogram grouped the two most dominant species,
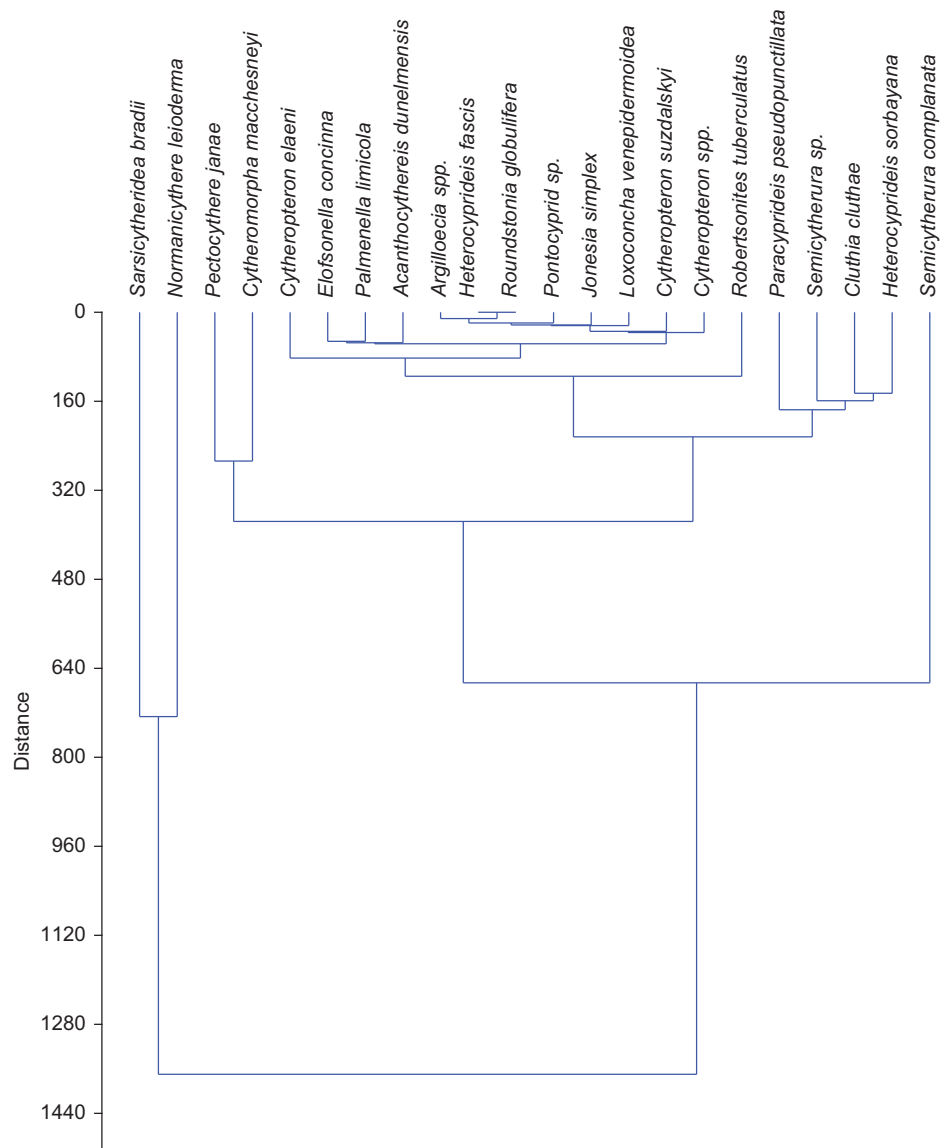
Fig. 3. Cluster analysis with a Euclidean similarity measure of 21 species of ostracodes in the northern Bering Sea, 1976–2010. (*Loxoconcha* was very rare in a few samples and is not included in the total species count of 21.) This grouping sorts species with similar patterns of abundance.

N. leioderma and *S. bradii,* as a single separate node, based upon similar abundance patterns. Another cluster is linked from this one node to a second grouping, which includes some euryhaline species, such as *Heterocyprideis fascis* and *Paracyprideis pseudo-punctillata. P. janae* and *C. macchesneyi* also grouped together. Finally, several relatively uncommon species clustered together including *Cytheropteron elaeni* and *Robertsonites tuberculatus.*

3.3. Distributions of dominant taxa in the Arctic Ocean and North Pacific

The dominant taxa we found in the northern Bering Sea have been identified living in other areas of the Arctic, as well as subarctic and temperate regions. We used the ~700-sample Modern Arctic Ostracode Database (Cronin et al., 2010a; 2010b) collected over the past 50 years to provide some context for our collections. *N. leioderma, S. bradii* and *S. complanata* are polar species and are found on continental shelves along the Chukchi–Beaufort and

Laptev–Kara Sea margins (Fig. 4A–C). The most abundant species observed in all years in the northern Bering Sea (except 2004, when only limited samples were available) was *N. leioderma*. Compared to the Bering Sea, it also occurs with less frequency in the Chukchi–Beaufort Sea region at water depths of 10–80 m, comprising up to 30% of the ostracode fauna there. *S. complanata* is relatively rare in the western Beaufort and Chukchi Sea and is more common along Siberian shelves (Stepanova et al., 2007). *S. bradii* occurs in the Chukchi and Beaufort Seas, usually comprising between 20% and 40% of the assemblage at depths of 0–50 m.

In contrast, *Pectocythere* is primarily a more temperate genus that inhabits subarctic regions in the Pacific Ocean, such as the Gulf of Alaska (Brouwers, 1990). *P. janae* inhabits the Bering Sea in varying abundances depending on the year, occurring in higher abundances during relatively warmer temperatures. It has been reported in the high Arctic only in low numbers in a few samples in the western Beaufort Sea collected in 1969 and 1970 and in the East Siberian Sea in Chaunskaya Bight Inlet, a warm refugium inhabited by a number of species common to the Bering Sea (E.
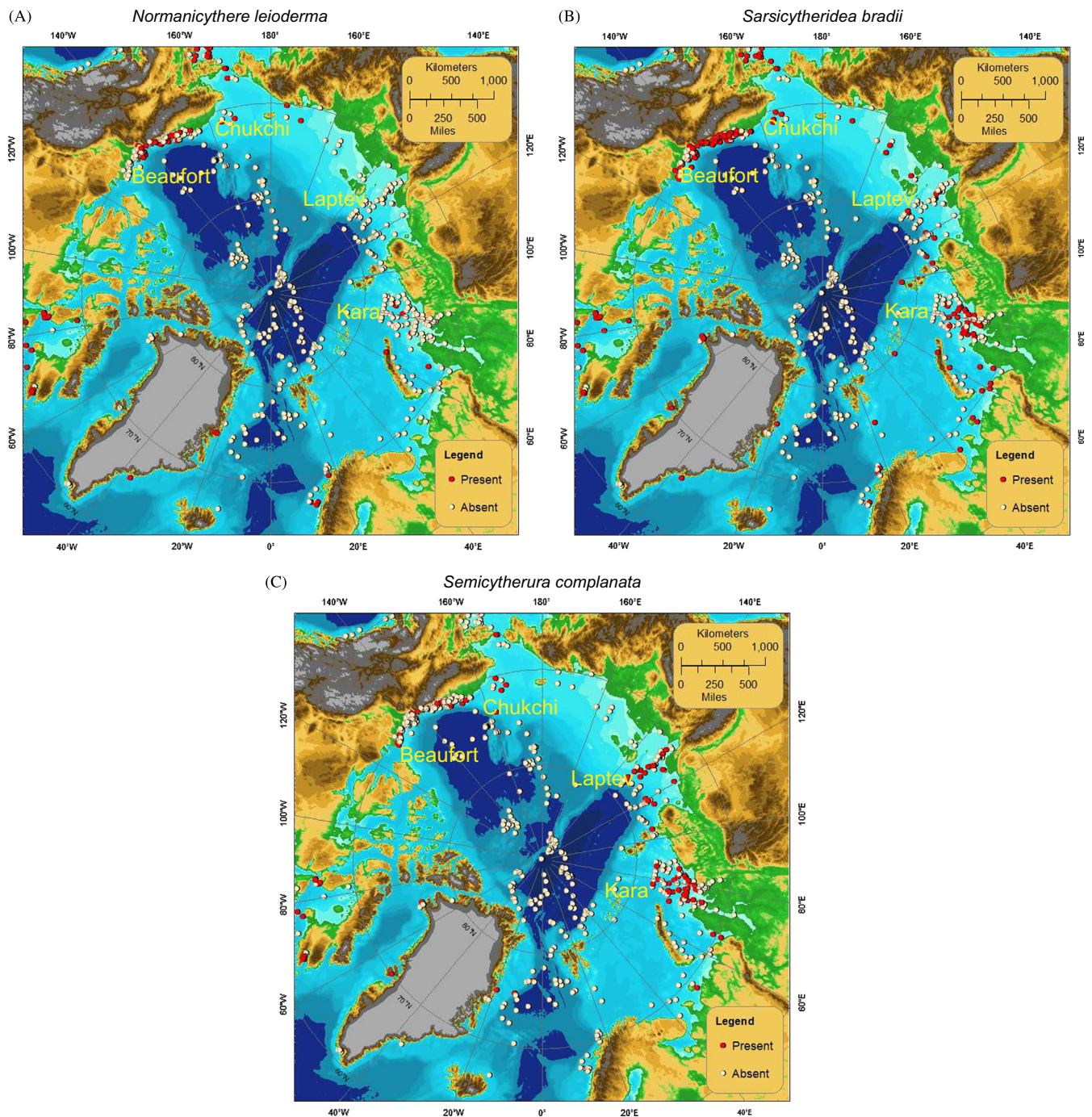
(A) *Normanicythere leioderma*

(B) *Sarsicytheridea bradii*

(C) *Semicytherura complanata*

Fig. 4. (A–C) Modern Arctic distribution and abundance of three key cryophilic species, *Normanicythere leioderma* (a), *Sarsicytheridea bradii* (b), and *Semicytherura complanata* (c), based on a ∼700-coretop sediment sample database (the Modern Arctic Ostracode Database, MAOD). The red circles indicate species presence, white circles absence. The MAOD provides census data for approximately 100 species of benthic marine Ostracoda from modern surface sediments collected over the last 50 years from the Arctic Ocean and adjacent seas (Cronin et al., 2010b).

Schornikov, personal communication, 2012). *P. janae* is absent in other parts of the East Siberian Sea (E. Schornikov, personal communication). It has not been reported in the Laptev, Kara, Barents, Norwegian, or Greenland Seas. Although its precise temperature tolerance is not constrained, this species is clearly not a circum-Arctic, cryophilic species like others found in the Bering Sea assemblages, and is only found in the Bering and the Arctic (Chukchi–Beaufort and Eastern Siberian Seas) during

periods with warmer water temperatures. We note here that W.M. Briggs (personal communications) considers *P. janae* to be a synonym of *Kotoracythere arctoborealis*.

3.4. Temporal trends in Bering Sea indicator species

We plot the relative proportions (percent abundance of each species out of the total assemblage) for four key species for each
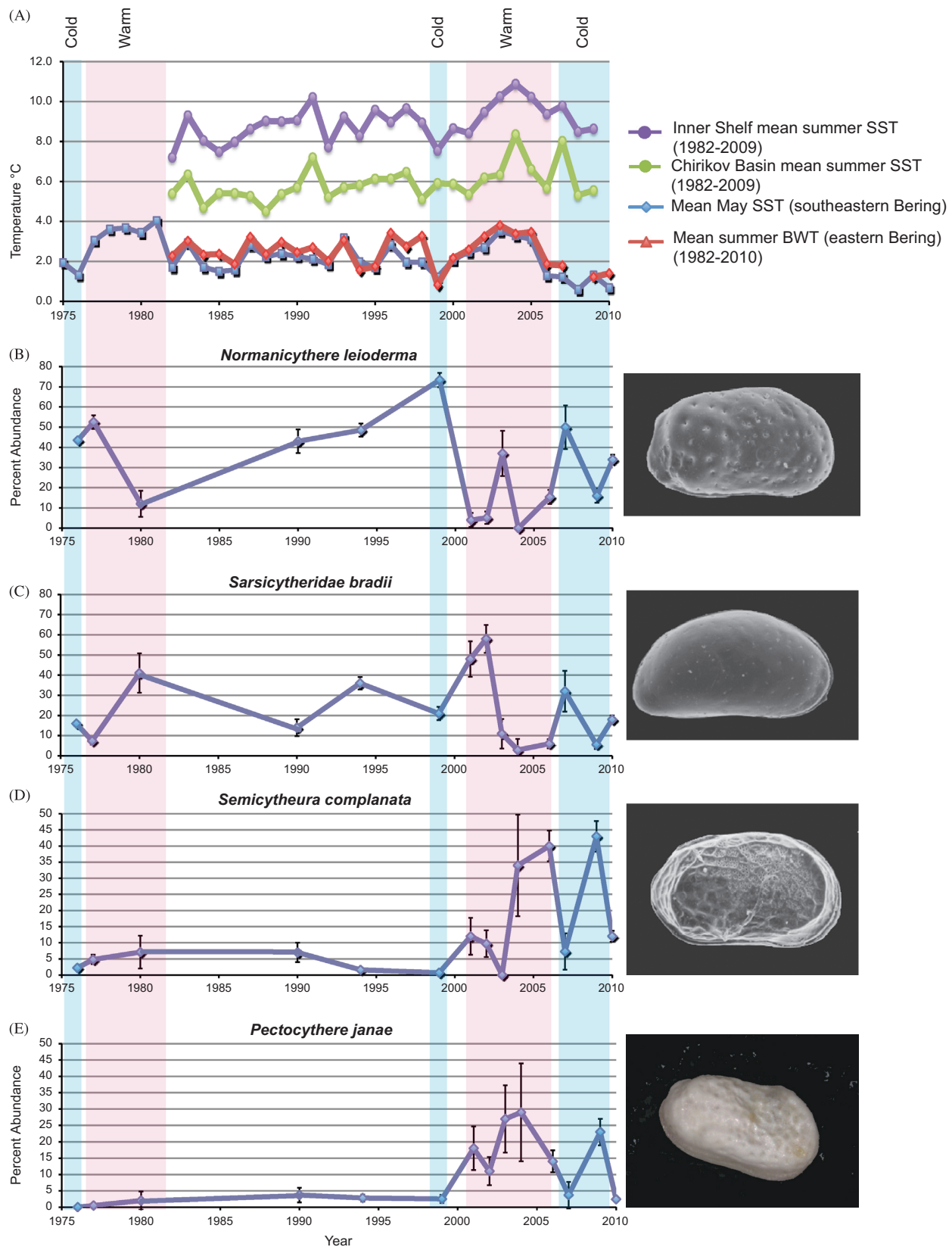
Fig. 5. (A) Chirikov Basin and Inner Shelf mean summer sea-surface temperature (SST) from 1982 to 2009 (purple and green lines). In order to have a temperature record that encompassed the study's time period, we include May SST (blue line) for the southeastern Bering since 1975 and summer BWT (red line) for the eastern Bering since 1982. Because the central-northern Bering Sea is shallow (< 50 m) and well mixed, SST and BWT patterns generally show similar decadal patterns but do not provide year- and site-specific temperature data for our exact study region or precise temperature range that ostracode species require. May SST and BWT data are correlated ($r^2 = 0.82$; $p < 0.001$) for the period 1982–2003. (Data from http://www.beringclimate.noaa.gov/data/). (B–E) Plots of abundances of the four most common species in the Bering Sea, 1976–2010. (Photos courtesy of A. Stepanova and *Pectocythere* photo by L. Gemery.) Results represent the relative abundance of the major taxa out of the entire population for each year. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)

year in which samples were available from 1976 to 2010 (Fig. 5B–E). (Samples from the Norton Sound area in 1978 were not plotted in this analysis because these samples were collected in a river plume and are not representative of the central Bering area assemblage.) These abundance data were evaluated with respect to averaged BWT and May SST data (Fig. 5A). May SST is a good predictor for the summer bottom temperature, based upon a regression analysis of the two variables, ($r^2 = 0.82$; $p < 0.001$) for the period 1982–2003. Confidence limits on ostracode abundance data were generated using the binomial methods of Buzas (1990).

N. leioderma (Fig. 5B) comprised 40–50% of the Bering assemblages in 1976–1977 before declining to 10% during warming in the late 1970s/early 1980s. *N. leioderma* increased in abundance during the 1980s and 1990s, peaking at $> 70\%$ abundance during the cold year of 1999. This species decreased to a minimum in the early 2000s, as temperatures warmed between 2000 and 2005 and then increased again in abundance during the cooler period since 2006.

S. bradii (Fig. 5C) comprised between 8% and 60% of Bering Sea ostracode assemblages from 1976 to 2002, followed by a sharp decline in 2003–2006, apparently in response to warmer temperatures. The decline, however, lagged the near-immediate decline of *N. leioderma* by a year or two.

Based on our observations of morphological variability in *S. complanata* (Fig. 5D) throughout the Arctic and subarctic, it appears that this is a species that may include several subspecies living in cold temperate to Arctic regions, with each having a different temperature tolerance. Bering Sea populations of *S. complanata* comprised $< 10\%$ of assemblages during the late 1970s through 1999, followed by an increase to 30–40% during 2004–2006.

In contrast to some of the cryophilic species discussed above, *P. janae* is typically absent to very rare ($< 4\%$ of assemblages) in the northern Bering Sea from 1976 to 1999 (Fig. 5E). During the interval 2001–2006, it increased to 10–30% of northern Bering assemblages as water temperatures increased.

3.5. Canonical correspondence analysis for Bering Sea species

A canonical correspondence analysis (CCA) is a standard form of correspondence analysis that allows environmental data to be incorporated into the analysis. It was used to examine the frequencies of ostracode species in relation to several environmental variables that may influence their overall abundance (Fig. 6; Park and Cohen, 2011; Torres Saldarriaga and Martínez, 2010). The five most abundant species were evaluated in the context of the following variables: (1) surface air temperature (SAT, the air temperature at 2m height above the ocean surface, as derived from the NCEP/NCAR reanalysis model) in the Chirikov Basin (Z. Brown, personal communication); (2) SAT along the Inner Shelf (Z. Brown, personal communication); (3) the Arctic Oscillation Index (http://www.beringclimate.noaa.gov/data/); (4) May SST in the southeastern Bering Sea (http://www.bering-climate.noaa.gov/data/), and (5) the number of open water days in the Chirikov Basin and Inner Shelf (Brown et al., 2011). Only samples containing ≥ 20 total specimens ($n=77$) were used in this analysis (see Buzas, 1990 for sample size reasoning). Considering that ostracode density was low, we decided that a criterion of ≥ 20 specimens per sample would provide a sufficient indication of the dominant species living in the area. Our reasoning was that a higher cutoff would have eliminated too many sample sites from the available data pool and would have prevented a broader regional characterization. We concluded that the 20-specimen threshold optimally balances the competing demands of describing representative population structure and geographic coverage. We recognize that due to this threshold, not all the rare species are enumerated statistically, but the number of samples ($n=77$, 4923 specimens) in the study vicinity helps to validate general community composition. Finally, we note that the 1978 data were excluded from the CCA because those samples were collected from shoreline locations and corresponded to much lower salinity conditions.

The CCA shows that the frequency of *P. janae* is associated with high SATs, or in general, warmer temperatures, indicating a
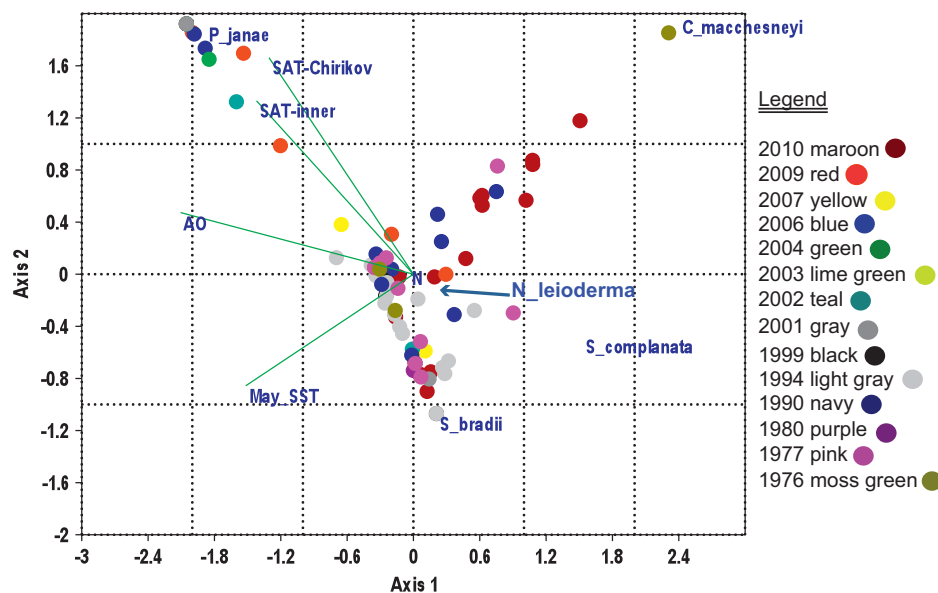

Fig. 6. Canonical correspondence analysis (CCA) results of five dominant Bering Sea ostracode species frequencies ($n=77$) in relation to several environmental variables (surface air temperature [SAT] in the Chirikov Basin, SAT along the Inner Shelf, the Arctic Oscillation Index, May sea surface temperature [SST] in the southeastern Bering Sea) that may influence their overall abundance and distribution. The green vector lines show the environmental variables and the quadrant and samples with which they are associated. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)

distinct ecological niche for *P. janae* because of the high degree of separation within its own quadrant in the CCA plot. Samples from the year 2010 (maroon circles) are in the opposite quadrant from the SAT vectors and *P. janae*, consistent with colder water temperatures in 2010. Samples from 1994 (light gray circles) cluster together because in that year *S. bradii* and *N. leioderma* represented 36% and 49% of the total ostracode population, respectively. A few samples from 1977 and 1976 (pink and army green circles) are located in lower salinity waters of Norton Sound and correspondingly group with *C. macchesneyi*, a species that can tolerate reduced salinity. Several samples in 2010 (maroon circles) contained higher proportions of *C. macchesneyi* as well. Data corresponding to *N. leioderma* is centrally distributed in the plot, meaning that it is abundant in many of the samples in most years. Computed eigenvalues show that axis one (80%) and axis two (15%) account for a combined 94% of the variance in this analysis.

3.6. Chukchi Sea ostracode assemblages

In the Chukchi Sea, we identified a total of 28 species from eight surface sediment samples collected in 2009 and eight samples from 2010, representing a mixture of Arctic and subarctic species (Fig. 7). The most abundant species in the Chukchi Sea were *P. pseudopunctillata* (17% in 2009 and 16% in 2010) and *S. bradii* (27% in 2009 and 8.4% in 2010). Although the Chukchi shelf has many species in common with the Bering Sea, *N. leioderma* was less abundant in the Chukchi (0.8% in 2009 and 11% in 2010); *P. janae* comprised 7.8% in 2009 and 5.1% in 2010. Ostracode density averaged 1.6 ostracodes per dry gram of sample.

3.7. Detrended Correspondence Analysis (DCA) of ostracodes from the Bering, Chukchi, Beaufort, Laptev, and Kara Seas

We performed a detrended correspondence analysis (DCA) of ostracode samples from Bering Sea and Arctic Ocean shelf surface sediments in order to evaluate the similarity of Bering Sea ostracode assemblages to those living on Arctic continental shelves. DCA is commonly used to analyze similarities and dissimilarities among faunal and floral assemblages. We used the PAST DCA software application and included surface samples from our Chukchi and Bering Seas study and samples from the Beaufort, Kara, and Laptev Seas contained in the MAOD database (Cronin et al., 2010a; 2010b). A total of 306 samples containing 43,220 ostracode specimens were used in the DCA. We excluded samples with < 20 specimens and samples from water depths ≥ 200 m to constrain the analysis to continental shelf samples.

The plot of the first and second principal components, which accounts for 51% of the variance, shows a distinct clustering of the Bering Sea samples and a clustering of the Arctic samples (Fig. 8). These results indicate that the Bering Sea samples differ from the Arctic samples in having larger proportions of *N. leioderma* and *S. bradii* and much lower proportions of *P. pseudopunctillata*.

4. Discussion

During the 34-year time span of this study, we found that two primary assemblages inhabited the northern Bering Sea. One assemblage is dominated by Arctic species (i.e. *N. leioderma*, *S. bradii*), and the other has greater proportions of temperate-subarctic species (i.e. *P. janae*). These two end-members are evident in Fig. 9A–D during the relatively cool years 1994 and 1999 and warm years 2000–2006. These data suggest that *P. janae*

and *S. complanata* prefer warmer conditions (Fig. 9A and B). The CCA (Fig. 6) further suggests that *P. janae* has a distinct warmer temperature preference, as it plots in its own quadrant and is positively correlated with SAT. We hypothesize that *P. janae* survive and possibly migrate, with the help of strong northward currents, in the Bering Sea in greater numbers during these warm periods. Marine ostracode species migrate in response to climatic changes, including changes in ocean temperatures and water masses over glacial–interglacial and millennial timescales (Didié and Bauch, 2000). However, the rates at which populations can migrate in response to short term temperature changes (i.e. interannual to decadal) is poorly known. Our data suggest that populations of *P. janae* and perhaps other species may have been able to increase in population, either through migration, higher
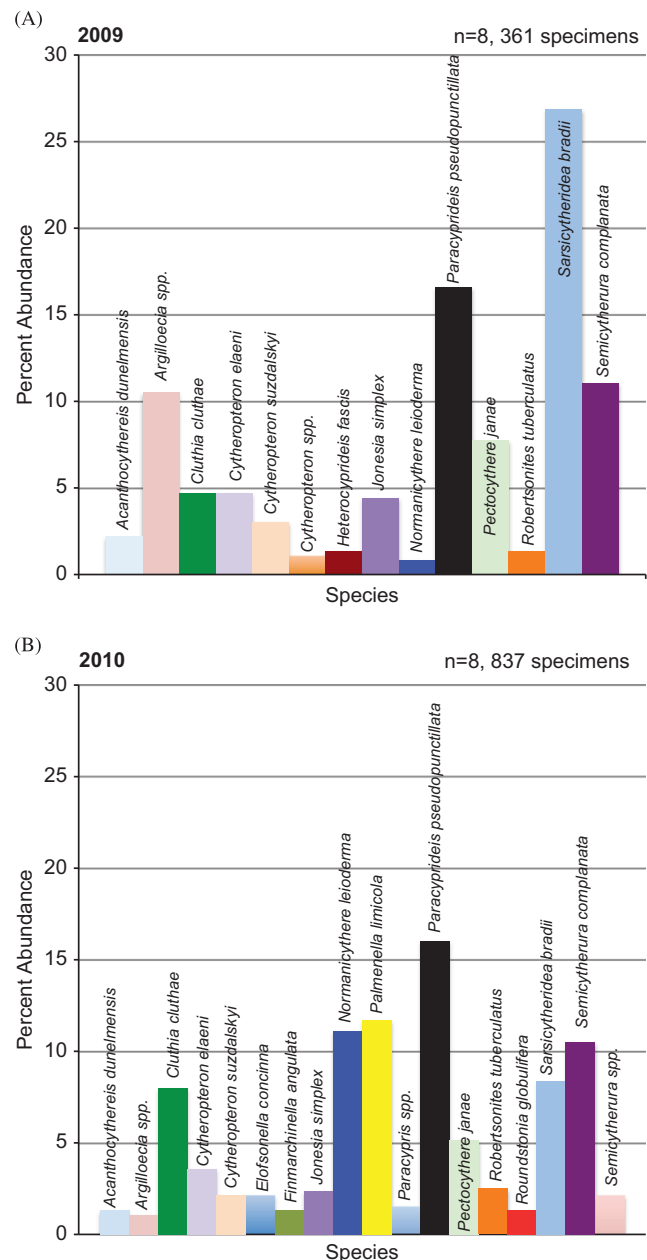

Fig. 7. The Chukchi Sea ostracode assemblages in 2009 and 2010. Bar plots include species that composed > 1% of the total population.
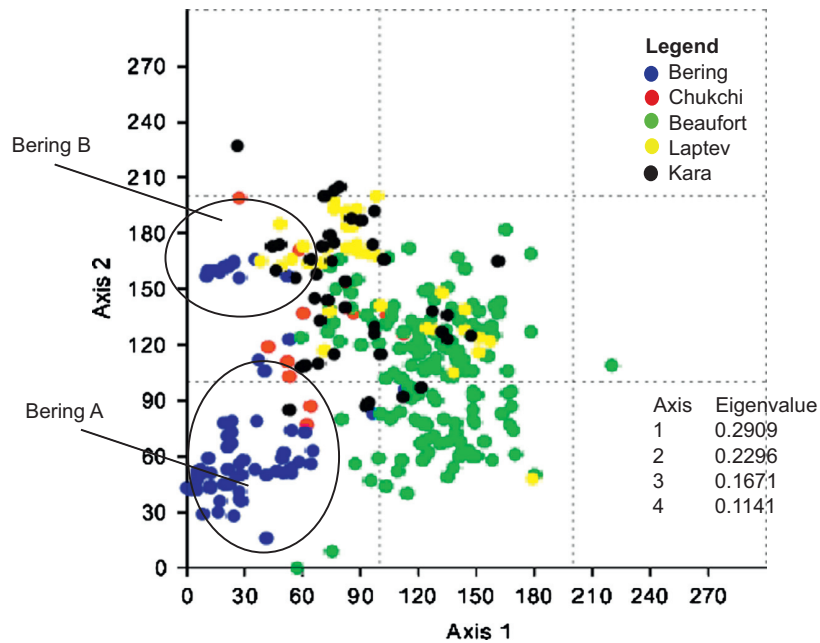
Fig. 8. Detrended correspondence analysis (DCA) results on shallow-water ostracode abundances in samples from the Bering (blue dots) and Arctic (Chukchi [red dots], Beaufort [green dots], Laptev [yellow dots], and Kara [black dots]) ($n=306$, 43,200 specimens). (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)

reproduction rates or alternately enhanced survival in parts of the Bering Sea over relatively short timescales. Additional study is needed to clarify the mechanisms for increased abundance of particular species. For example. *P. janae* may have higher reproduction rates with warmer temperatures, leading to higher abundance during warm years. During 2004–2006, *S. complanata* reached a maximum of 40% abundance of the total ostracode population, suggesting a preference for warmer water and/or minimal sea ice (Fig. 5C). Further work is needed to establish the significance of this variation in *S. complanata* abundance with respect to Bering Sea oceanographic patterns.

In contrast, *N. leioderma* and *S. bradii* clearly decline in abundance in warm years (Fig. 9C,D). These patterns support prior studies that show water temperatures are critical for survival and reproduction in many marine ostracodes (Brouwers, 1988; Hazel, 1970).

This study also provides insight into the ostracode faunal composition of shallow, continental shelf areas in the Bering Sea and Arctic Ocean proper. The subarctic Bering Sea assemblage (Fig. 8, blue circles) contains different dominant species than the Arctic assemblages in the Chukchi, Beaufort, Laptev and Kara Seas, which had many more species in common. Fig. 8 further reflects that the Chukchi assemblage (red circles) is intermediate in position between the subarctic and Arctic assemblages, representing some mixing of species.

The greater proportion of *N. leioderma* found in the Bering Sea is the key difference between subarctic and Arctic populations. Although Stepanova et al. (2010) found this species in a few shallow samples in the Kara Sea, occurring at depths of less than 50 m, *N. leioderma* is present outside the Arctic and seems to prefer subarctic ecosystems. For example, it occurs in shallow coastal waters of the Atlantic and Atlantic-influenced Arctic: Gulf of St. Lawrence (Norman, 1869), Iceland (Elofson, 1941), eastern Ellesmere Island (Brady and Norman, 1896), western Greenland (Stephensen, 1938), St. Margaret's Bay, Nova Scotia (Levings, 1975) and the Gulf of Maine (Blake, 1933). Hazel (1970) classified *N. leioderma* as an amphi-Atlantic species (i.e. a species that occurs on both eastern and western margins of the Atlantic) ranging in depth from 3 to 150 m in the frigid-cold climate zone,

which coincides with the Arctic-Nova Scotian biogeographic province. Hazel (1970) specifically noted that summer survival and reproductive temperatures control *N. leioderma's* population. This agrees with our data showing a decline in *N. leioderma* during warmer periods in the northern Bering Sea.

Additionally, the DCA plot indicates separation between two groups of the Bering Sea samples, which we term as "Bering B" and "Bering A". Bering A samples plot low on axis two due to larger proportions of *N. leioderma* and *S. bradii*. Together these two species comprised up to 94% of the total Bering Sea ostracode assemblage during colder years between 1976 and 2010. They were less common during years in which northern Bering Sea summer bottom temperatures were >0–$2\,^\circ$C. *S. bradii*, which reaches $>50\%$ of the community composition in the Bering Sea, was less common in the Chukchi Sea (27% maximum in 2009 and 8.4% in 2010) as was *N. leioderma* (0.8% in 2009 and 11% in 2010). In contrast to the Beaufort Sea and Chukchi Sea where it is common (17% in 2009 and 16% in 2010), *P. pseudopunctillata* comprised only 2% of the total Bering Sea assemblage. The Bering B group contained larger proportions of *S. complanata* in samples collected in 2006 and 2009.

5. Conclusions

This study provides the first faunal survey and time-series examination of ostracode assemblages in the Bering Sea. We conclude that the relative dominance of Arctic and subarctic species in the Bering Sea has changed during the last several decades as ocean temperatures fluctuated, illustrating the potential use of ostracodes to characterize ocean water mass changes in the region. We hypothesize that these faunal changes reflect either the direct effects of temperature or other temperature-related factors, such as reduced sea ice. Data from the two research cruises that collected Chukchi Sea ostracodes are not extensive enough to assess temporal change, but can serve as a baseline for future study.
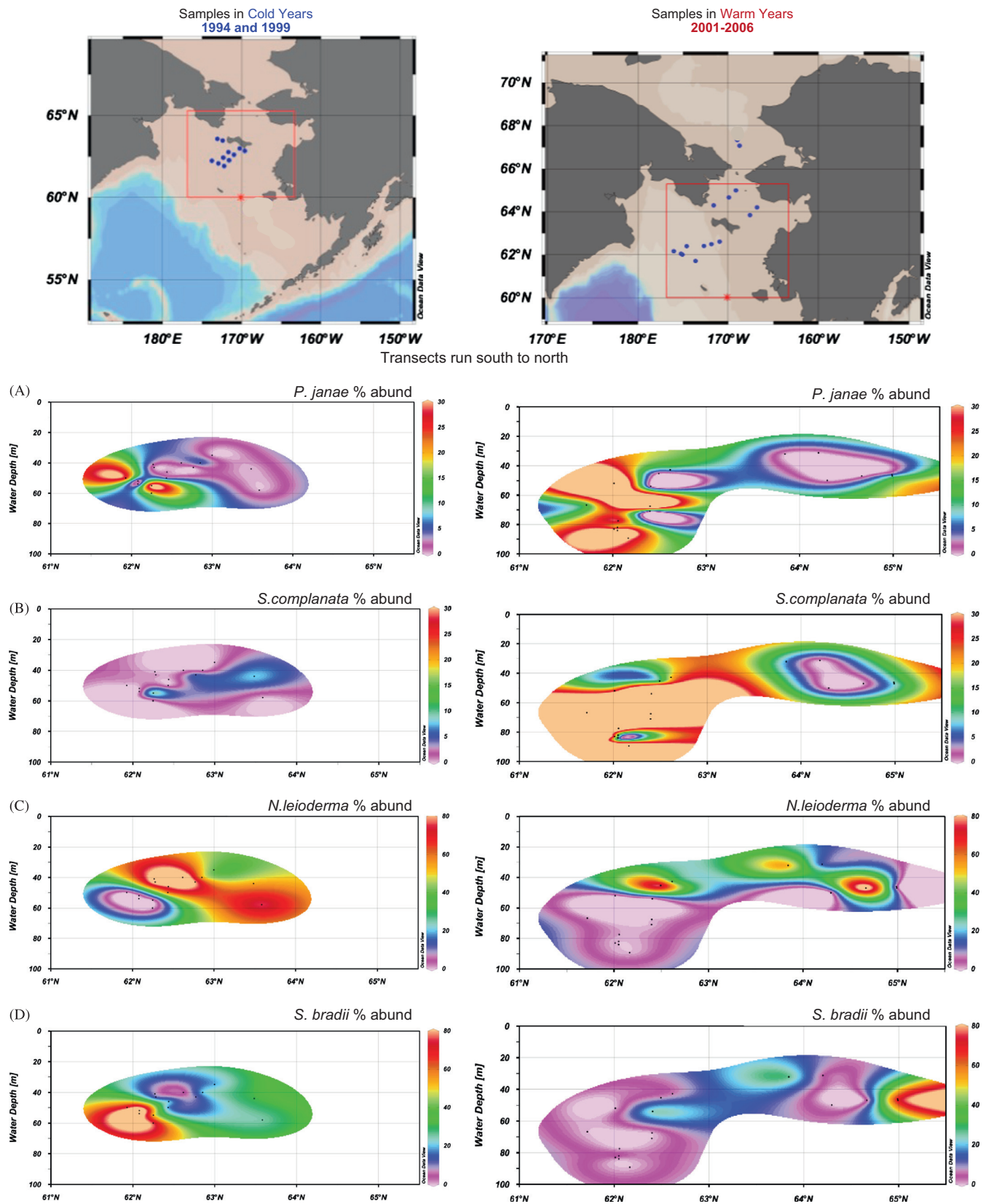
Fig. 9. A–D: Contour plots comparing species abundance in cold years (1994 and 1999) vs. warm years (2001–2006) north and south of St. Lawrence Island. Maps (top) show central-northern Bering shelf study area (red square) and locations of samples (blue dots) in the years represented. Contour plots show abundance of key taxa from a south–north transect. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)

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